

A Comparison of the Species Richness and Trophic Roles of Gastropods and Chitons on Rocky Shores of Temperate and Tropical West America

by

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Abstract. I examined local species richness and trophic roles of gastropods and chitons in rocky intertidal zones in Oregon, U.S.A., and in Costa Rica, Central America. Local species richness was quite variable. Tropical sites did not always have more species nor was there a significant difference in local species richness between regions. However, the species pool for the tropical transects (75) was larger than for Oregon (44). The density of individuals per square meter was much greater in the temperate sites.

Between-habitat diversity differences may account for most of the increase in over-all gastropod species richness in Costa Rica. A regression analysis suggests that, among the variables tested, only the number of gastropod refuges explains a significant amount of the variation in local species richness among all sites.

An increase in carnivorous and carrion-eating snail species accounts for most of the expansion in species richness in Costa Rica. This increase is principally in species that eat different food resources than do temperate zone snails (*e.g.*, sipunculans and small fishes) and species that feed on polychaetes, gastropods, and dead or injured animals.

INTRODUCTION

MANY TAXA OF plants and animals, including gastropods (THORSON, 1952; KOHN, 1971), have an increasing number of species along a decreasing latitudinal gradient (PIANKA, 1966). This ecological phenomenon has been the focus of many studies, and several hypotheses based on physical and biological processes have been developed to explain the generation and maintenance of this pattern (PIANKA, 1966; PIELOU, 1975; HUSTON, 1979).

One interesting question about this diversity pattern is whether specific tropical habitats have a greater diversity than similar habitats in the temperate zone. If so, what ecological processes allow more species to co-occur in the tropical habitats? Are there simply additional, different microhabitats present within these "similar habitats" in the tropics compared to the temperate zone? Are important resources (such as food and habitat) more finely partitioned? Have physical and/or biological disturbances (*i.e.*,

predation) kept species populations reduced in size so that episodes of interspecific competition, if they occur at all, are brief?

The general purpose of this study was to examine quantitatively rocky intertidal areas in Oregon and Costa Rica in order to provide answers to the following questions:

A. How does the gastropod and chiton species richness in rocky intertidal areas differ between temperate and tropical regions of West America?

B. What physical factors might explain some of the variation in species richness between these areas?

C. Do tropical carnivorous gastropods use food resources differently than temperate snails?

SITE DESCRIPTIONS AND METHODS

Table 1 describes the study sites chosen to sample areas with different wave exposures and topographies. The Oregon sites were studied from April to August, during 1970, 1971, and 1972, the Costa Rican sites, in January and February, 1972.

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Table 1

Description of the exposed-coast rocky intertidal study sites in Oregon and Costa Rica.

Locality	Tidal range	Transect name (abbreviation)	General description
Cape Arago, Oregon, U.S.A.	2.1 m	North Cove (NC) Middle Cove 1 (MC1) Middle Cove 2 (MC2) South Cove (SC)	cliff with high splash pool ledge area with no loose boulders boulder field bedrock with ledges and loose boulders
Cape Blanco, Oregon, U.S.A.	2.2 m	Cape Blanco 1 (CB1) Cape Blanco 2 (CB2)	bedrock with ledges and loose boulders bedrock with ledges and loose boulders
Playa Hermosa, Guanacaste, Costa Rica	2.7 m	Playa Hermosa 1 (PH1) Playa Hermosa 2 (PH2) Playa Hermosa 3 (PH3)	bedrock with ledges and loose boulders bedrock with ledges and loose boulders bedrock with ledges
Sámara, Guanacaste, Costa Rica	2.7 m	Sámara 1 (S1) Sámara 2 (S2) Sámara 3 (S3)	flat bedrock, ledges, and loose boulders flat bedrock, ledges, and much algal turf flat bedrock with ledges and tidepools
Quépos, Puntarenas, Costa Rica	2.5 m	Quépos 1 (Q1) Quépos 2 (Q2)	large boulders bedrock with ledges and loose boulders

At each site, I chose a point at the high-tide drift line and placed the base point for a transect a random number (between 0 and 50) of meters from this point along the drift line. I stretched a metric tape from the base point toward the water's edge at low tide and placed quadrats (1 m × 1 m) across the transect line at arbitrarily set intervals according to the length of the transect and the time available to complete the work. For instance, South Cove was sampled every meter along the transect line, while at Sámara 3, the interval was every 5 m. Within each quadrat I counted all snails, chitons, and nudibranchs and noted their positions (under rocks, on top of rocks, etc.). I did not include vermetid snails and octopuses. Due to difficulties in differentiating the numerous small *Fossarus* spp. from the similarly shaped and marked *Littorina aspera* in Costa Rica, I lumped these species. I had similar problems distinguishing *Collisella paradigitalis* from *C. digitalis* in Oregon so I lumped them together. When *Fossarus* spp., *Littorina* spp., and limpets occurred in high numbers, I counted them within six 10-cm² quadrats placed randomly within the 1-m² quadrat and extrapolated their densities to 1 m² from the average of these counts.

I quantified the intertidal height above 0-m low tide at 20-cm intervals on the transect line within each sampled quadrat using a simple surveying technique (placing a pole on the transect line and sighting a horizontal line from a marked position on this pole, a flag on a stationary pole a known distance above the 0-m tide point, and the horizon). Based on C. M. Yonge's method of zonation (RICKETTS *et al.*, 1968), I used 174 cm above mean lower low water (0-m tide) as the separation height between high and mid intertidal zones for Oregon. Since tropical intertidal areas are not as well studied and the tidal datum is different (mean low water spring tides), I based the separation height between high and mid intertidal zones in Costa Rica on gastropod assemblages. I determined it

to be the lowest height reading (120 cm) of the quadrats that contained only those gastropod species (*Littorina aspera*, *L. modesta*, *Nerita funiculata*, *N. scabricosta*, *Planaxis* spp., *Tegula pellisserpentis*, *Purpura pansa*, and *Acanthina brevidentata*) whose distributions are limited to the high intertidal zone and the extreme upper portions of the mid intertidal zone (KEEN, 1971; SPIGHT, 1976; GARRITY & LEVINGS, 1981).

I quantitatively or qualitatively estimated some physical factors that might influence species richness. I qualitatively estimated wave exposure (0.0 = lowest exposure to waves; 1.0 = greatest exposure) for each transect by observing surf conditions and by assessing the number and size of loose rocks. Using the average height measurements for each quadrat, I computed the proportion of quadrats that occurred below the high intertidal zone in each transect (Quépos 1 was excluded due to sampling problems). As a measure of the availability of gastropod refuges, I computed for each transect the proportion of quadrats in which snails were found on the undersides of rocks or ledges.

Since all of the values of these variables vary between 0 and 1, I angularly transformed them before computing a stepwise multiple regression with species richness. I included a latitude variable in this analysis, computed as a ratio of the transect's latitude divided by 90°; I also angularly transformed this ratio.

The diets of the carnivorous and carrion-eating gastropods were determined from a literature review (MILLER, 1974), from field observations, and by collecting individuals in the field, isolating them in containers of sea water for up to 24 h, and then microscopically examining fecal pellets for prey hard parts. I assigned the carnivorous snail species to various diet categories based on the percentage of occurrence of specific food items in their diets. If 75% or more of the food items in a species' diet were in one

Table 2

A comparison of the species richness and density of gastropods and chitons in the Oregon and Costa Rican transects.

	Oregon						Costa Rica									
	NC	MC1	MC2	SC	CB1	CB2	PH1	PH2	PH3	S1	S2	S3	Q1	Q2		
Number of quadrats	8	14	14	51	19	13	14	15	13	23	25	32	14	9		
Species richness	13	18	28	36	19	22	27	28	15	33	34	29	38	26		
$\bar{X} \pm \text{SEM}$			22.7 \pm 3.34							28.8 \pm 2.43						
U-test							N.S.									
Number/m ²	61	83	171	188	143	140	341	47	105	49	28	34	46	18		
$\bar{X} \pm \text{SEM}$			131.0 \pm 20.2							83.5 \pm 37.9						
U-test							U = 40, P < 0.05									

diet category, I assigned that species only to that diet category. If less than 75% of the feeding observations were in one category, I assigned the species to the two diet categories that made up at least 70% of the diet. If the two most common diet categories comprised less than 70% of the observations, I included the third highest diet category.

MILLER (1974) lists the chiton and gastropod species discussed in this study as well as their abundances and the diets of the carnivorous and carrion-eating snails. These lists may be obtained from the author. Voucher specimens reside in the author's collection.

RESULTS

Species Richness

The number of species of gastropods and chitons is extremely variable in both Oregon and Costa Rica (Table 2). The number of species found in a local area does not differ significantly between regions. The density of gastropods and chitons is, however, significantly greater in the Oregon transects.

The species pool for the Oregon samples (44) is much smaller than that for the Costa Rican samples (75); thus, there is an increase in the number of gastropod species with decreasing latitude when large geographic areas are considered.

Physical Factors

In an attempt to ascertain what physical factors might explain some of the variation in species richness among the transects, I compiled a list of potentially important variables (Table 3) that I was able to quantify or qualitatively estimate.

I chose wave exposure (WAVES) as a variable since the degree of exposure of an intertidal area to wave shock is important in determining what kinds of organisms occur there (RICKETTS *et al.*, 1968). I picked the proportion of

samples from below the high intertidal zone in a transect (HT) as a variable because there is a trend of increasing species richness with a decrease in intertidal height (JOHNSON, 1970; MILLER, 1974; SPIGHT, 1977). The presence of undersides of rocks, boulders, or ledges increases the topographic complexity of an area and provides microhabitats for the snails that are more sheltered from mortality factors like desiccation and wave shock than areas with only flat bedrock (KOHN & LEVITEN, 1976; MENGE & LUBCHENCO, 1981). For this reason, I calculated a refuge variable (REF) by computing the proportion of quadrats in each transect that had undersides of rocks or ledges occupied by gastropods. I included latitude (LAT) as a variable since it could include some biological and physical parameters that are different in the tropics compared to the temperate zone, but which I did not measure (PIANKA, 1966; HUSTON, 1979).

Although not a physical factor, I also used the number of sampled quadrats (QUADS) as a variable since, at least for Oregon, species richness (S) may be related to it in my study ($S = -8.66 + 25.8 \log \text{QUADS}$; $t = 3.21$, $P < 0.025$; $R^2 = 0.72$). For Costa Rica, none of the regression analyses using log-transformed or untransformed values of S and QUADS resulted in a significant regression or an R^2 value greater than 0.14.

A comparison of each of the variables in Table 3 for a significant difference between Oregon and Costa Rica indicated that only "Latitude" was significantly different ($U = 48$, $P < 0.001$).

I did a stepwise multiple regression using these variables to find out which ones might explain significant amounts of the variation in species richness (S) among all of the transects (excluding Quépos 1). The largest total adjusted R^2 , 0.83, was obtained using the logarithm of species richness; the only significant independent variable was the gastropod refuge variable ($F = 6.0$, $P < 0.05$). The regression equation was: $\log S = 0.004 \text{ QUADS} - 0.003 \text{ LAT} + 0.003 \text{ REF} + 0.001 \text{ HT} - 0.002 \text{ WAVES} + 1.319$.

Table 3

Summary of the physical factor measurements and estimates, the latitudes, and the sample sizes of the Oregon and Costa Rican transects.

Transect	Wave exposure	Proportion of quadrats below high intertidal zone	Proportion of quadrats with gastropod refuges	Latitude	Number of 1-m ² quadrats sampled
Oregon					
North Cove	1.00	0.27	0.00	43.32°	8
Middle Cove 1	0.80	0.38	0.14	43.32°	14
Middle Cove 2	0.40	0.75	1.00	43.32°	14
South Cove	0.40	1.00	0.53	43.32°	51
Cape Blanco 1	0.80	0.70	0.26	42.50°	19
Cape Blanco 2	0.80	0.92	0.54	42.50°	13
Costa Rica					
Playa Hermosa 1	0.60	0.57	0.50	10.50°	14
Playa Hermosa 2	0.60	0.84	0.40	10.50°	15
Playa Hermosa 3	0.80	0.60	0.08	10.50°	13
Sámara 1	0.20	0.89	0.35	9.87°	23
Sámara 2	0.40	0.97	0.60	9.87°	25
Sámara 3	0.20	1.00	0.19	9.87°	32
Quépos 1	0.80	—	0.79	9.45°	14
Quépos 2	0.80	0.94	0.67	9.45°	9

The Between- and Within-Habitat Components of Diversity

Total diversity in a large geographic region consists of two components: within-habitat diversity and between-habitat diversity (MACARTHUR, 1965). If within-habitat diversity has contributed significantly to the larger species pool in Costa Rica, then similar habitats should support more diverse assemblages of gastropods and chitons there than in Oregon. Two lines of evidence in my study suggest that the within-habitat component is not as important as the between-habitat component for rocky intertidal habitats.

First, transects in Oregon and Costa Rica that are similar in wave exposure, proportion of quadrats below the high intertidal zone, and proportion of quadrats with gastropod refuges (Table 3) have similar diversities (Table 2)—*e.g.*, South Cove and Sámara 2; Cape Blanco 2 and Quépos 2. Second, the number of species found in individual 1-m² samples is not significantly different between the two regions ($U = 37.5$, $P > 0.05$). These values ranged from 4.1 to 7.8 ($\bar{X} = 5.8 \pm 0.59$ SEM) in Oregon and from 2.8 to 5.3 ($\bar{X} = 4.4 \pm 0.29$ SEM) in Costa Rica.

Between-habitat diversity appears to be different between regions. To assess this, I compared for each region the percentages of (1) omnipresent species, (2) species found in all transects except one, and (3) species unique to one transect (Table 4). These results suggest that transects in Oregon have more species in common and have fewer unique species. This may mean that the transects

are sampling similar habitats in Oregon and more different habitats in Costa Rica.

Comparison of the percentages of the species in each transect that are also found in one or more other transects (SALE, 1980) also suggests an increase in the between-habitat component in Costa Rica. Oregon transects have significantly greater percentages than Costa Rica ($U = 44.5$, $P < 0.01$). The average percentage is 93.1% for Oregon transects and 88.3% for Costa Rican transects.

Trophic Structure

In the trophic structure analysis, I lumped carnivorous and carrion-eating snails together since I could not tell whether snails known to feed on carrion would also eat living prey. Some snails that normally attacked living prey were observed eating dead animals.

Table 4

A comparison of the percentage of species found in all transects, the percentage in all transects except one, and the percentage unique to one transect.

	Oregon	Costa Rica
% omnipresent	9.1%	2.7%
% in all but one transect	34.1%	10.7%
% unique	29.5%	36.0%

Table 5

Comparison of the trophic characteristics of the assemblage of species in each transect.

	NC	MC1	MC2	SC	CB1	CB2	PH1	PH2	PH3	S1	S2	S3	Q1	Q2
No. herbivorous species	10	12	20	22	12	14	14	17	10	22	21	13	20	13
$\bar{X} \pm \text{SEM}$			15.0 \pm 2.0							16.2 \pm 1.6				
No. carnivorous and carrion-eating species	3	6	8	14	7	8	13	11	5	11	13	16	18	13
$\bar{X} \pm \text{SEM}$			7.7 \pm 1.5							12.5 \pm 1.4				
Proportion of carnivorous and carrion-eating individuals	.06	.03	.03	.06	.06	.05	.07	.37	.05	.15	.33	.54	.27	.28
$\bar{X} \pm \text{SEM}$			0.05 \pm 0.01							0.26 \pm 0.06				

The assignment of some of the grazing mollusks to the carnivorous or herbivorous trophic level is difficult since some species may be indiscriminate grazers, feeding on both plant and animal material. For instance, some species of *Calliostoma* graze on sessile animals (MILLER, 1972; PERRON, 1975); but I did not find animal remains in the feces of seven *C. ligatum* from the Oregon transects. Except for *Placiphorella velata*, which entraps and eats mobile crustaceans (MCLEAN, 1962; Miller, personal observation), most chitons graze on plant material (references in MORRIS *et al.*, 1980). However, there is evidence that some species of *Mopalia* graze on sessile animals and algae (BARNAWELL, 1960). In this study I have considered all chitons except *P. velata* as herbivores, *C. ligatum* as an herbivore, and all species of *Cypraea* as carnivores.

There is no significant difference in the number of herbivorous species found in transects in Oregon compared to Costa Rica (Table 5; $U = 29$, $P > 0.05$). However, Costa Rican transects have significantly more carnivorous and carrion-eating species than Oregon ($U = 38$, $P < 0.05$). The Costa Rican transects also have a larger proportion of carnivorous and carrion-eating individuals than Oregon transects (Table 5; $U = 44.5$, $P < 0.01$). The proportion of carnivorous and carrion-eating species in the species pool is 0.41 in Oregon and 0.52 in Costa Rica.

The Diets of Carnivorous and Carrion-Eating Snails

Since the increase in species richness in Costa Rica occurs primarily in carnivorous and carrion-eating species,

I examined the diets of these snails to compare food-resource use between temperate and tropical species (Table 6). The main differences are threefold increases in the number of snail species eating polychaetes and gastropods in Costa Rica compared to Oregon and the exploitation by tropical snails of sipunculans and fishes, two food types not used by Oregon gastropods.

There is also a large increase in species eating dead material in the tropics, due mainly to the numerous species of Columbellidae. Most columbellids are attracted to dead and/or injured prey (MARCUS & MARCUS, 1962; SPIGHT, 1976; HATFIELD, 1979; Miller, personal observation), but not enough work has been done to show that columbellids are only carrion-eaters.

DISCUSSION

I examined the gastropod and chiton species richness at several similar, exposed-coast rocky intertidal zone sites in Oregon and Costa Rica. Local species richness is quite variable (Table 2). The tropical transects were not always richer nor was there a significant difference in the number of species found in Oregon and Costa Rican transects. However, the density of gastropods and chitons was significantly greater in the temperate areas (Table 2). The total number of different gastropod and chiton species in all Costa Rican transects (75) is much larger than in all Oregon transects (44).

These results agree with SPIGHT's (1977) comparisons of prosobranch species richness at two Washington State rocky intertidal locations and one Costa Rican site. The

Table 6

Number of carnivorous and carrion-eating gastropod and chiton species feeding in each diet category. * Indicates that species exist but were not found in my samples.

	Sponges	Coelen- terates	Sipun- culans	Poly- chaetes	Live, mobile crusta- ceans	Bar- nacles	Bi- valves	Gastro- pods	Bryo- zoans	Echino- derms	Tuni- cates	Fishes	Para- sitic	Dead animals
Oregon	3	2	0	4	1	5	3	1	1	0*	1	0	2	3
Costa Rica	1	1	2	13	0*	7	3	4	0	1	1	1	1	10

difference in the number of tropical prosobranch species in Spight's study (79) and mine (61) may be due to his deliberate sampling of as many habitats as possible at this one site (SPIGHT, 1976, 1977). It is possible that the Cape Arago region in Oregon, where I found 25 prosobranch species, has more habitats than the more wave-protected Puget Sound area (Shaw Island) in Washington, where Spight found 16 prosobranch species.

The between-habitat component of species diversity appears to contribute more than the within-habitat component to the larger total species richness that I found in Costa Rica. This suggests that I was sampling a greater diversity of habitats in Costa Rica and agrees with SPIGHT's (1977) conclusion that there are more niches (defined by substratum and intertidal height) in Costa Rica with no temperate zone counterparts.

Although many different physical and biological factors may control local species richness, the only significant variable of those that I measured or estimated as explaining significant amounts of variation in species richness (Table 3) was the presence of gastropod refuges. The availability of the undersides of rocks and ledges as shelters from wave shock, UV radiation, insolation, desiccation, and large, visual predators has also been found by others to be important in controlling species diversity and population sizes (KOHN & LEVITEN, 1976; JOKIEL, 1980; MENGE & LUBCHENCO, 1981).

The most obvious differences between the trophic structure in Oregon and Costa Rica are the significant increases in the tropical region in the number of species of carnivorous and carrion-eating gastropods and in their proportion of the total individuals. The number of herbivorous gastropod and chiton species per transect is also greater in Costa Rica than in Oregon, but not significantly. Three of the tropical carnivorous snail species use food resources present in the Oregon rocky intertidal but not eaten by Oregon snails (sipunculans and fishes) and a large number (13) prey on polychaetes. There are also substantial increases in the number of snail species eating living gastropods (4) and dead or injured animals (10) in Costa Rica.

Although the more diverse carnivorous gastropod assemblage in Costa Rica has large numbers of species sharing some food resources (at least on a large scale) and other species eating prey not consumed by Oregon species, I do not have enough dietary information to conclude that competition has been more important in structuring the gastropod community in Costa Rica than in Oregon compared to some of the other possible structuring forces, such as predation (MENGE & LUBCHENCO, 1981).

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